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COWBIRD SELECTION OF BREEDING AREAS: THE ROLE OF HABITAT AND BIRD SPECIES ABUNDANCE

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ABSTRACT.—We investigated the use by Brown-headed Cowbirds (*Molothrus ater*) of five forest edge types and the forest interior of Green Ridge State Forest in the ridge and valley physiographic province of Maryland. Habitats were sampled, and breeding birds counted at each site. Cowbirds were detected in all habitats except forest interior; occurring most frequently in forest-brush (50.0% of points), -stream (46.3%), and -powerline (33.3%) edges. Among edge types, snag BA was also significantly ($P < 0.01$) higher at forest-powerline, -brush, and -stream edges than at forest-open road and -closed road edges. These habitats had high total vegetation volume (TVV), with which bird and host species abundances were positively associated. However, high TVV was not always indicative of high snag BA. With all habitats combined, bird species abundance, total vegetation volume (TVV), and foliage height diversity (FHD) at a height of 1–2 m were significantly ($P < 0.05$) higher at points where cowbirds were detected than at those where they were not detected, however only bird species abundance remained significant ($P = 0.059$) when forest interior was removed from the analysis. We propose that cowbirds in western Maryland select breeding areas based on: (1) distinct visible edges formed by canopy openings in the forest landscape, (2) occurrence of both high snag BA and high TVV at the forest edge, and (3) presence of high bird species abundance. *Received 17 Aug. 1996, accepted 20 Mar. 1997.*

Birds nesting near habitat edges often are subjected to increased brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Gates and Gysel 1978, Brittingham and Temple 1983). Cowbirds also have been found deep within the interior of large blocks of forest, presumably searching for host nests (Chasko and Gates 1982, Verner and Ritter 1983, Gates and Giffen 1991, Hahn and Hatfield 1995). Many Nearctic-Neotropical migrants require large blocks of forest for successful reproduction and survival (Robbins 1979, Whitcomb et al. 1981, Wilcove 1988, Robbins et al. 1989). However, these forests often are fragmented (Askins 1994). We investigated the relationship between cowbird use of different forest edge types and the forest interior of a large public forest in western Maryland. First, we characterized and compared habitat types and their corresponding bird species abundances with their use by cowbirds for breeding. Secondarily, we evaluated the relationship of different habitat characteristics and corresponding bird species abundances on the selection of breeding areas by cowbirds by comparing areas where cowbirds were present with those where they were absent.

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STUDY AREA AND METHODS

Study area and plot selection.—We conducted this study on the 15,699 ha Green Ridge State Forest (GRSF) in eastern Allegany County, Maryland, in the ridge and valley physiographic province (Stone and Matthews 1977). GRSF is the most contiguous block of state forest in western Maryland. Elevations range from approximately 152 m along the Potomac River to about 620 m on the highest ridge. The managed forest landscape forms a mosaic of different anthropogenic features, forest types, and successional stages. Permanent corridors through the forest are formed by several road and utility rights-of-way, as well as natural stream corridors.

We sampled six habitat types: forest-powerline edge (N = 18), forest-open canopy road edge (N = 28), forest-closed canopy road edge (N = 29), forest-brush edge (N = 28), forest-stream edge (N = 28), and forest interior (≥250 m from an opening, N = 29). Forest-road edges included five open canopy and six closed canopy roads. Open canopy (canopy cover at road center <10%) roads were generally dirt and gravel, and averaged 6.0 m (±0.38 SE, N = 28) wide. Closed canopy (canopy cover at road center >90%) roads were primarily dirt, and averaged 3.7 m (±0.38 SE, N = 29) wide. Brush areas at forest-brush edges were characterized by clearcuts ranging in age from 1–10 years and in size from 2.1–23.2 ha. We included forest-stream edges along six different second order streams. Streams were 5.5 m (±0.61 SE, N = 28) wide, with an overhead canopy cover of 83-99%. The powerline corridor, averaging 45.9 m (±1.4 SE, N = 18) wide, was characterized by low shrubs, herbaceous areas, wildlife food plots, and brambles near the forest edge. Management included mowing of grass areas late in the summer by the Maryland Dept. of Natural Resources and selective herbicide application to woody vegetation by the Potomac Edison Company.

We spaced sample points to maximize independence and minimize the effects of canopy openings other than those under study. Forest-powerline edge points were separated from each other by at least 200 m; all other points were separated from each other by at least 250 m. Canopy openings other than those under study had to be ≥250 m from a sample point; therefore, not every point along a particular edge was suitable. Points were often 500 m or more apart. Locations of sample points along edges began with an initial random point followed by subsequent points along the edge; points within forest interior were randomly located.

Methods.—We made counts within a 4-h period beginning at sunrise from 20 May–26 June 1995. On average, six points representing different habitat types were counted within each time period. Sample order of habitats was rotated each day to minimize temporal biases. Point counts were done at the forest edge or boundary, except for interior points, and lasted for 10 min. An additional 10 min was specifically devoted to the detection of cowbirds (20 min total). Counts began once the sample point was reached. Bird species heard or seen at a point were tallied during the count. Counts were not conducted during rain or prolonged drizzle, heavy fog, or when wind speeds exceeded 20 kph (Robbins 1981). Point count data forms were a combination of unlimited-radius and spot-mapping methods, allowing us to mark the location of birds seen or heard in relation to the sample point and forest edge.

Habitat data were collected at sample points from 12 June–20 July 1995. The understory complexity of each plot was determined using a variation of the vertical-line intercept method (MacArthur and Horn 1969). A metric measuring rod, 18 mm in diameter × 3-m long, was used to measure total vegetation volume (TVV) (Mills et al. 1991). It was placed vertically at 2-m intervals along a 20-m straight line transect. When sampling an edge, the transect was bisected by and oriented perpendicular to the edge boundary. We counted the number of decimeter sections that contained vegetation within a 1-dm radius of the rod.

Total vegetation volume was calculated using the formula: TVV = h/10p in m^3 of vegetation/m^2 units; where h = the total number of hits in all layers at all points, and p = the total number of points. An index of foliage height diversity (FHD) was calculated by treating each meter section as a vegetation layer and using the Shannon-Weiner index $H' = -\Sigma p_i \ln p_i$, where p_i = the proportion of total hits in the ith layer. Other habitat data collected at each end (0 and 20 m) of the 20 m transect and at the sample point (10 m) included tree basal area (BA, m^2/ha) divided into deciduous, conifer, and snag (angle gauge); canopy cover (%, spherical densiometer); and vegetation height (>5 m, range finder).

Within each habitat, we calculated bird species richness using the rarefaction method (Krebs 1989) and bird and host species abundance (detections/count), leaving out the cowbird. All variables were tested for normality and, except for bird species abundance, were found not to be normally distributed. A two-way independent *t*-test and an analysis of variance (ANOVA) were used to test for differences between cowbird present (i.e., detected) and cowbird absent (i.e., not detected) points and among habitats, respectively, for bird species abundance. Variables that could not be normalized were tested using a Mann-Whitney-Wilcoxon test or a Kruskal-Wallis (KW) one-way analysis of variance based on ranks. Forest interior was removed from tests used to evaluate differences in habitat characteristics among edge habitats. If a KW or ANOVA test showed a significant difference, then an appropriate multiple comparison test was used to determine which habitats were significantly different (Siegel and Castellan 1988, StatSoft, Inc. 1994). Comparisons were also made using log-linear analysis to determine the significance of interactions among variables, especially bird and host species abundance, habitat type, and edge TVV. All statistical tests were performed using STATISTICA (StatSoft, Inc. 1994).

RESULTS

We made 1980 observations of 60 bird species, including 34 known cowbird hosts. Brown-headed Cowbirds were detected in all habitat types, except forest interior. The rank order of cowbird occurrence in edge types was forest-brush (50.0% of points), -stream (46.4%), -powerline (33.3%), -open road (14.3%), and -closed road (10.3%) edges. The cowbird ranked eleventh (2.6%) in overall species abundance, and varied from eighth most abundant in forest-brush and -stream edges to fourteenth most abundant in forest-closed road and -open road edges. Based on rarefaction, bird species richness varied from 32.0 species at forest-stream edge to 39.2 species at forest-brush edge (Table 1). Host species comprised 56.7% of all species and 77.7% of all observations. Host species richness was lowest in forest-closed road edge with 17.0 species, and highest in forest-brush and -powerline edges, both with 20.3 species (Table 1). There was no significant ($P > 0.05$) difference among habitats in bird or host species richness.

The forest-powerline edge had the highest mean bird species abundance, followed by -brush, and -open road edges (Table 1). Mean bird species abundance for forest-powerline, -brush, and -open road edges were significantly ($P < 0.05$) higher than at forest-stream, -closed road, and interior (Table 1). Mean host abundance was significantly ($P < 0.05$) higher at forest-powerline and -open road edges than forest-stream, closed

TABLE 1

MEANS (±SE) OF BIRD AND HABITAT VARIABLES SAMPLED AT THE COUNTING POINT, I.E., FOREST EDGE, BY HABITAT AT GREEN RIDGE STATE FOREST, MARYLAND

	Interior (N = 29)	Closed road (N = 29)	Open road (N = 28)	Powerline (N = 18)	Stream (N = 28)	Brush (N = 28)
Bird variable						
Species richness (rarefaction)						
Bird ($E[S_{200}]$)	34.1	33.2	38.1	36.8	32.0	39.2
Host ($E[S_{180}]$)	18.0	17.0	18.7	20.3	17.5	20.3
Abundance (#/point)						
Bird	10.00 ± 0.45^{b}	10.59 ± 0.46^{b}	13.11 ± 0.56^{a}	15.28 ± 0.53^{a}	11.18 ± 0.41^{b}	13.54 ± 0.49^{a}
Host	7.66 ± 0.34^{c}	8.66 ± 0.36^{bc}	10.25 ± 0.55^{a}	11.83 ± 0.55^{a}	9.75 ± 0.45^{bc}	9.96 ± 0.44^{ab}
Habitat variable						
Vegetation height (m)	21.62 ± 0.63^{b}	22.33 ± 0.42^{b}	17.92 ± 0.86^{c}	20.71 ± 0.94^{bc}	26.57 ± 0.77^{a}	22.14 ± 0.77^{b}
Basal area (m^2/ha)						
Deciduous	33.97 ± 1.83^{a}	22.93 ± 1.37^{b}	11.79 ± 1.65^{c}	22.50 ± 2.66^{b}	24.46 ± 2.26^{b}	21.07 ± 1.37^{b}
Coniferous	5.35 ± 1.59^{a}	0.52 ± 0.35^{b}	4.64 ± 1.23^{a}	1.11 ± 0.76^{b}	3.57 ± 1.58^{a}	0^{b}
Snag	2.93 ± 0.91^{b}	0.35 ± 0.35^{c}	0.54 ± 0.40^{c}	4.17 ± 1.16^{a}	2.32 ± 1.11^{b}	3.04 ± 0.79^{b}
Foliage height diversity (H′)						
0–1 m	0.17 ± 0.02^{b}	0.20 ± 0.02^{b}	0.27 ± 0.01^{a}	0.26 ± 0.02^{a}	0.17 ± 0.02^{b}	0.23 ± 0.02^{ab}
1–2 m	0.03 ± 0.02^{c}	0.09 ± 0.03^{bc}	0.14 ± 0.03^{b}	0.09 ± 0.03^{bc}	0.11 ± 0.03^{b}	0.20 ± 0.03^{a}
2–3 m	0.07 ± 0.03^{bc}	0.09 ± 0.03^{bc}	0.10 ± 0.03^{bc}	0.02 ± 0.02^{c}	0.14 ± 0.03^{ab}	0.22 ± 0.03^{a}
Total	0.39 ± 0.05^{b}	0.47 ± 0.04^{ab}	0.60 ± 0.04^{a}	0.62 ± 0.06^{a}	0.61 ± 0.05^{a}	0.54 ± 0.04^{ab}
Total vegetation volume (m^3/m^2)	0.41 ± 0.05^{c}	0.60 ± 0.05^{bc}	0.95 ± 0.09^{a}	0.99 ± 0.10^{a}	0.79 ± 0.08^{ab}	0.96 ± 0.08^{a}

^{abc} Dissimilar letters indicate statistical significance ($P < 0.05$) among habitat types.

TABLE 2

NUMBER AND PERCENTAGE (%) OF BIRDS DETECTED WITHIN ADJACENT CORRIDOR OR BRUSH OPENING (>5 M FROM THE EDGE), ALONG FOREST EDGE (±5 M FROM THE EDGE), AND WITHIN THE FOREST (>5 M FROM THE EDGE)

Forest edge type	Within opening		Along edge		Within forest	
	No.	%	No.	%	No.	%
Closed canopy road	1	0.3	280	88.9	34	10.8
Open canopy road	0	0.0	273	71.6	107	28.4
Powerline	51	18.1	156	54.7	75	27.2
Stream	0	0.0	259	80.7	62	19.3
Brush	150	38.6	147	38.1	89	23.3

road, and interior (Table 1). Mean host abundance was significantly ($P < 0.05$) higher at forest-brush edge than interior; forest-brush edge was not significantly ($P > 0.05$) different from the other edge habitats (Table 1). Forest interior had the lowest bird and host species abundances on average. When in edge habitats, birds were detected most often close to the boundary between adjacent habitats, particularly if bordered by a road or stream (Table 2).

Total vegetation volume profiles along a transect by habitat showed a similar pattern among habitats across the forest side of a transect (0–8 m), whereas TVV at the sampling point (edge or 10 m) and across the opening side of an edge (12–20 m), if present, differed among habitats (Fig. 1). Total vegetation volume was significantly ($P < 0.01$) higher in forest-powerline, -open road, and -brush edges than -closed road edge and interior (Table 1). Total vegetation volume was significantly ($P < 0.05$) higher in forest-stream edge than interior, but did not differ between any other habitat (Table 1). Mean foliage height diversity (FHD) was significantly higher at forest-powerline, -open road, and -stream edges than forest interior (Table 1). Forest-brush and -closed road edges were not significantly ($P > 0.05$) different from other habitats. Foliage height diversity by height interval was significantly ($P < 0.05$) higher at 0–1 m in each habitat, except forest-brush and -stream edges, while levels 1–2 m and 2–3 m were similar (Table 1). Foliage height diversity was similar among meter layers for both forest-brush and -stream edges (Table 1).

Although there were significant ($P < 0.05$) differences among habitats at the sampling point (10 m) for vegetation height, deciduous BA, and coniferous BA, the only obvious relationship to cowbird use, or lack thereof, was exhibited by deciduous and snag BA. Deciduous BA was significantly ($P < 0.05$) higher within forest interior than in any other

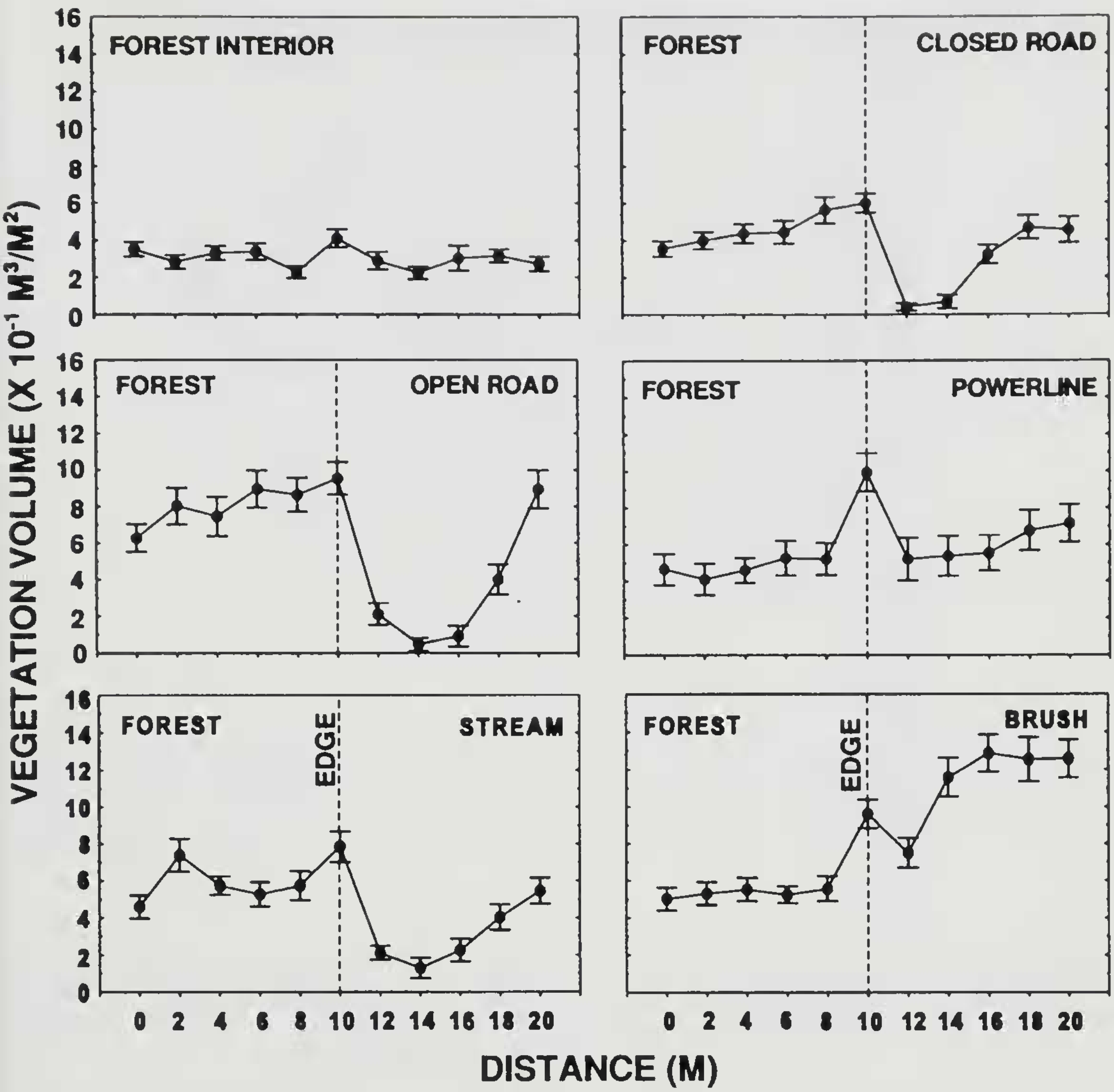

FIG. 1. Profile of mean (±SE) total vegetation volume from 0–3 m in height along a 20-m transect centered at the sampling point (10 m) within each habitat type. Except for forest interior, the transect was oriented perpendicular to the forest edge.

habitat type (Table 1). Snag BA was significantly ($P < 0.05$) higher at forest-powerline, -brush, interior, and -stream than forest-open road and -closed road (Table 1). There was generally a positive association between mean bird and host species abundance and mean TVV among habitats (Fig. 2). The response was similar for FHD. However, habitats where cowbirds were most frequently observed had both high mean snag BA and TVV (Fig. 3). Edge habitats with high mean snag BA had high mean TVV, but the reverse was not always true. Based on log-linear analysis, no relationships were detected ($P > 0.05$) among bird or host species abundance, TVV, habitat type, and cowbird occurrence. With all habitats combined, bird species abundance, TVV, and FHD at a height of 1–2 m

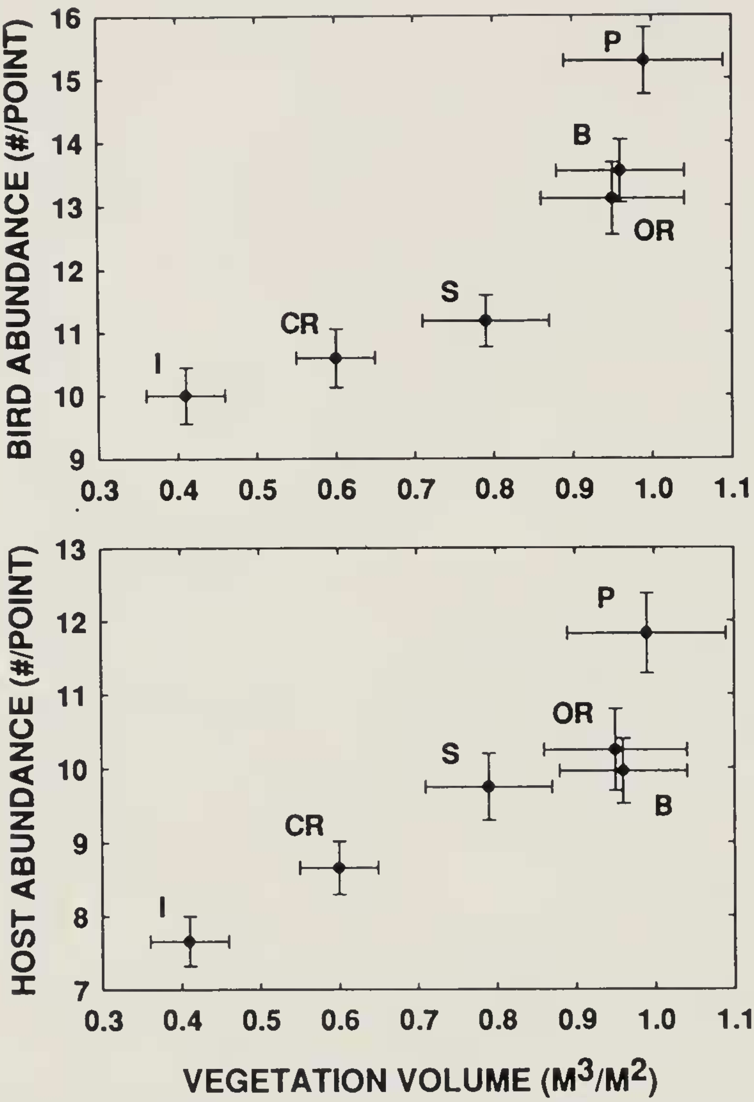

FIG. 2. The association between mean (±SE) total vegetation volume and mean (±SE) host and bird species abundances at the sampling point (10 m) within each habitat type. Habitat types are forest-brush (B), -stream (S), -powerline (P), -open road (OR), and -closed road (CR) edges and forest interior (I).

were significantly higher at cowbird present points than cowbird absent points (Table 3). However, with forest interior removed from statistical analysis and forest edge types grouped together, no significant ($P > 0.05$) difference between cowbird present and absent points occurred for host abundance, host species richness, TVV, FHD, or the abundance of any single host species. Only bird species abundance remained significantly ($P = 0.059$) higher at cowbird present points.

DISCUSSION

Because no habitat type within the anthropogenic forest landscape of western Maryland received 100% use, cowbirds in this particular region

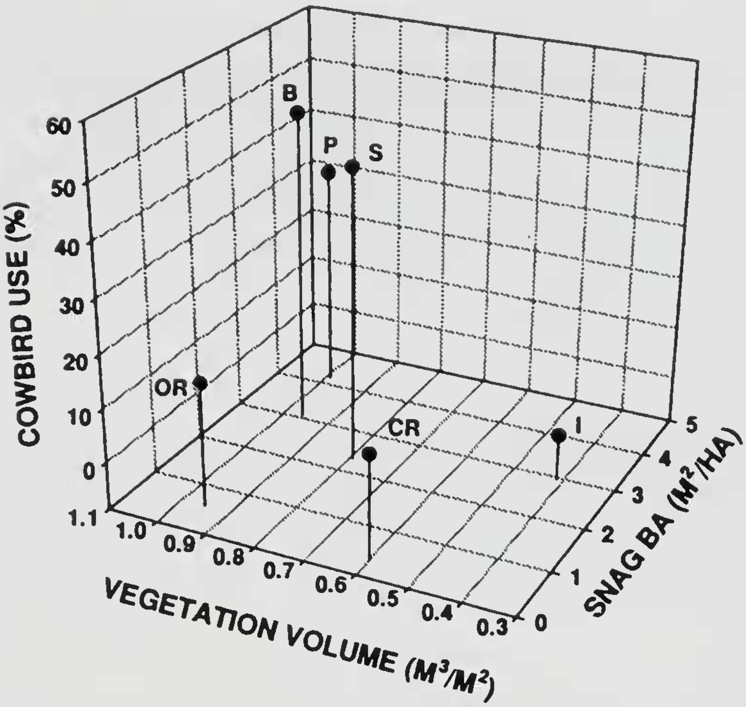

FIG. 3. The relationship between cowbird use of different habitat types and mean snag basal area and mean total vegetation volume at the sampling point (10 m). Habitat types are forest-brush (B), -stream (S), -powerline (P), -open road (OR), and -closed road (CR) edges and forest interior (I).

may be below the saturation level, selectively use only particular microhabitats, use microhabitats irregularly, or be present but undetected by an observer. However, the percentage of use of a particular habitat type should reflect its importance to cowbirds as a breeding area. Cowbirds were found near visible openings, ranging from narrow road and stream

TABLE 3

MEANS (±SE) OF VARIABLES SAMPLED AT COWBIRD PRESENT AND COWBIRD ABSENT POINTS AT GREEN RIDGE STATE FOREST, MARYLAND

Variable (units of measure)	Cowbird present	Cowbird absent	Test value
Bird species abundance[a] (detections/point)	13.23 ± 2.49 (40)	11.68 ± 3.10 (120)	2.85[**†]
Total vegetation volume (m^3/m^2)	0.90 ± 0.45 (40)	0.50 ± 0.43 (120)	−2.21[*]
Foliage height diversity for 1–2 m (H')	0.59 ± 0.25 (40)	0.51 ± 0.24 (120)	−2.05[*]

[a] Analyzed with an independent two-way *t*-test; all others with Mann-Whitney-Wilcoxon test. Sample sizes are in parentheses.

[*] $P < 0.05$; [**] $P < 0.01$; [†] significant at $P = 0.059$ when forest interior was excluded from analysis; all others not significant.

corridors to larger clearings, and not within closed-canopy forest interior. Brittingham and Temple (1983) also reported that cowbird occurrence, and thus an increased probability of parasitism, is highest near edges and openings. Both Rothstein et al. (1980) and Verner and Ritter (1983) found higher numbers of cowbirds in open canopy plots when compared with closed canopy plots. However, this pattern may vary among landscapes and among regions (Hahn and Hatfield 1995).

An increase in bird species diversity and abundance is often related to increased vegetation layering or the amount of vegetation present in an area (MacArthur and MacArthur 1961, Swift et al. 1984, Mills et al. 1991). This relationship is especially common near permanent edges and canopy openings where there is a large difference in canopy height between habitats. At forest edges in western Maryland, TVV tended to be higher several meters into the forest than that found in forest interior, probably due to increased light penetration to all foliage layers. Furthermore, at high contrast, shrubby forest edges, nests are often concentrated near the habitat discontinuity, perhaps making these areas more productive for cowbirds searching for host nests (Gates and Gysel 1978).

Still, cowbirds did not appear to respond solely to high TVV or FHD at a forest edge in choosing a breeding habitat with high bird species abundance. Instead, it appeared that both high numbers of snags, i.e., high snag BA, and high TVV were needed for a habitat to receive high cowbird use. If one or the other factor was low, than frequency of use was also low, e.g., forest-open road edges, or nonexistent, e.g., forest interior. In other regions, snags may be an attractant to cowbirds for use as a perch while locating nests (Norman and Robertson 1975, Anderson and Storer 1976, Robbins 1979). However, in a Wisconsin deciduous forest, Brittingham and Temple (1996) found that snags near a nest did not increase its probability of being parasitized. They did find a higher percent ground cover (0–0.5 m) and number of small shrubs and saplings (0.5–1 m) at parasitized nests, which would indicate high TVV.

In western Maryland, landscape and habitat characteristics were likely the most important factors used by cowbirds in selecting breeding areas. Although the use of habitat characteristics may aid cowbirds in selecting habitat types with high host abundance, other habitat types lacking a particular characteristic but having high host abundance may receive low use. This result may be more common in regions where cowbird populations are comparatively low. Therefore, it may not always be true that cowbirds concentrate in local areas where host densities are high (Johnson and Temple 1990). Furthermore, the cowbird has a generalized reproductive strategy that is relatively insensitive to host availability, resulting in little discrimination by females among small- to medium-sized passerines

(Mayfield 1965, 1977). We propose that cowbirds are attracted to distinct visible edges formed by canopy openings in the forest landscape and, secondarily, by the occurrence of both high snag BA and TVV. These function as proximate factors directing female cowbirds to those habitats with the potential for supporting high host nest density. Once the cowbird has settled near a forest edge, the observed abundance of bird species, i.e., their activity, is likely used to further refine selection of a suitable breeding area.

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